Cross-tolerance to abiotic stresses in halophytes: Application for phytoremediation of organic pollutants

Moez Shiri, Mokded Rabhi, Abdelhak El Amrani, Chedly Abdelly

Authors' names:

Moez Shiri[a,b], Mokded Rabhi[b*], Abdelhak El Amrani[a], and Chedly Abdelly[b]

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Authors' affiliations:

[a]: CNRS, Université de Rennes 1, UMR 6553, Ecosystèmes-Biodiversité-Evolution, 35042 Rennes cedex, France.

[b]: Laboratory of Extremophile Plants, Centre of Biotechnology of Borj Cedria, P.O. Box 901, 2050 Hammam-Lif, Tunisia.

[*]**Corresponding author:** Dr. Mokded Rabhi

E-mail: mokded.rabhi@gmail.com

Phone number: + 216 79 325 848

Fax number: + 216 79 325 638

Author Contributions Statement

Moez Shiri prepared the manuscript and Mokded Rabhi, Abdelhak El Amrani, and Chedly Abdelly discussed and revised it.

Abstract

Halopytes are plants able to tolerate high salt concentrations but no clear definition was retained for them. In literature, there are more studies that showed salt-enhanced tolerance to other abiotic stresses compared to investigations that found enhanced salt tolerance by other abiotic stresses in halophytes. The phenomenon by which a plant resistance to a stress induces resistance to another is referred to as cross-tolerance. In this work, we reviewed cross-tolerance in halophytes at the physiological, biochemical, and molecular levels. A special attention was accorded to the cross-tolerance between salinity and organic pollutants that could allow halophytes a higher potential of xenobiotic phytoremediation in comparison with glycophytes.

Keywords: genomic level, metabolomic level, physiological level, proteomic level, transcriptomic level.

Introduction

Halophytes are plants known for their ability to tolerate high salt levels in the soil. However, no clear definition was given to them and researchers still cannot certainly distinguish between halophytes and glycophytes. Flowers and Colmer (2008) call a halophyte any plant able to complete its seed-to-seed cycle at 200 mM NaCl or higher. Halophytes are considered to be rare plant species that arose separately in unrelated plant families during the diversification of Angiosperms (O'Leary and Glenn 1994; Flowers et al. 2010) similarly to epiphytes, saprophytes, xerophytes, aquatics, and marsh plants (Kremer and Van Andel 1995). They were estimated to constitute 1 to 2% of the flora (Flowers and Colmer 2008). Several fundamental and applied (economical) potential uses were attributed to halophytes as promising phytoresource. At the fundamental level, they help understand mechanisms involved in high salinity tolerance using morphological, anatomical, ultrastructural, physiological, biochemical, and molecular tools (Jithesh et al. 2006; Barhoumi et al. 2008; Smaoui et al. 2010; Rabhi et al. 2010b; Ellouzi et al. 2011; Debez et al. 2013; Ben Hamed et al. 2014). At the applied level, halophytes are used for food, fodder, forage, edible oil, biofuel, medicines, phytoremediation, phytodesalination, sandy soil fixation, ornamentation… (Khan and Qaiser 2006; Rabhi et al. 2010a, Rabhi et al. 2010d, Zaier et al. 2010; Al-Oudat and Qadir 2011).

Among several classifications of halophytes, a habitat-based one distinguishes between xerohalophytes, those thriving under saline arid conditions, and hydrohalophytes, those thriving under saline moist conditions (Al-Oudat and Qadir 2011). In their natural habitats, halophytes are simultaneously subjected to a multitude of abiotic stresses. However, data about pretreatment of halophytes with abiotic stresses such as draught, heavy metals, flooding, and nutrient deficiencies to enhance their tolerance to salinity are scarce. Recently, Ellouzi et al. (2013) investigated the responses of the halophyte *Cakile maritima* to increasing salt concentrations after pretreatment with three abiotic stresses: drought, salinity, and cadmium. They found that all pretreatments enhanced salt tolerance in this species through oxidative stress alleviation, in particular under severe salinity conditions. A seed priming with a relatively high $CaCl_2$ concentration (50 mM) was also shown to alleviate the adverse effects of high KCl, NaCl, Na_2SO_4, and $MgSO_4$ concentrations on germination of *Urochondra setulosa* (Shaikh et al. 2007).

In literature, there are more works about salt-enhanced tolerance to other abiotic stresses than about enhanced salt tolerance by other abiotic stresses in halophytes (See Ben Hamed et al. 2013). In *Artemisia anethifolia* and *Suaeda salsa*, salt adaptation enhanced PSII tolerance to heat stress through an improvement of

thermotolerance of PSII reaction centers, oxygen-evolving complexes, and light-harvesting complex (Lu et al. 2003). In *Hordeum maritimum*, it was also shown that moderate salinity alleviated the effects of phosphorus deficiency (Talbi-Zribi et al. 2012). Moreover, under low potassium availability conditions, salt stress improved K/Na selectivity in this halophyte (Hafsi et al. 2007). In the same context, Glenn et al. (2012) showed that salinity enhances *Atriplex* spp. tolerance to drought in drying soils. Beneficial salt effects on *Sesuvium portulacastrum* responses to drought (Slama et al. 2007) and heavy metals (Ghnaya et al. 2005; Zaier et al. 2010) were also reported. Salt priming was also shown to improve *Distichlis spicata* establishment under low to moderate salinity conditions (Sargeant et al. 2006).

Cross-tolerance is defined as the phenomenon by which a plant resistance to a stress induces resistance to another (Genoud and Metraux 1999). Because much of the injuries they induce in plants are associated with oxidative damage at the cellular level, oxidative stress tolerance is thought to play a key role in cross-tolerance to a variety of environmental stresses (Iseki et al. 2013).

1. Mechanisms involved in halophyte salt-induced tolerance are common to other abiotic stresses

2.1. Cross-tolerance physiology

2.1.1. Intracellular compartmentalization of toxic molecules and osmotic adjustment

As subjected to salt stress, halophytes compartmentalize excess ions predominantly in vacuoles, maintaining in this way their concentrations in the cytoplasm within tolerable limits. They accumulate organic osmolytes such as proline, glycinebetaine, and sugars mainly in cytoplasm for osmotic adjustment without impairing metabolic activities (Debez et al. 2010). This significantly contributes to the overall water relations that allow halophytes to obtain water from saline soils (Flowers and Colmer 2008). Osmolyte accumulation under salt-induced water deficiency was also observed in the case of direct (insufficiently-irrigated soil) and PEG- and mannitol-induced drought (Slama et al. 2007; Rouached et al. 2013). The comparison between *Hordeum martimum* and *H. vulgare* after 60 h of salt stress showed that the former is more able to accumulate inorganic solutes (such as Na^+) in vacuoles for osmotic adjustment and to keep organic solutes and a large part of K^+ for metabolic activities. Such an economic strategy was absent in *H. vulgare* whose osmotic adjustment was based on organic osmolytes regardless of stress severity (Yousfi et al. 2010). Munns (2002) reported that the use of one mole of Na^+, mannitol, proline, glycinebetaine, or sucrose as an osmoticum in leaf cell needs 3.5, 34, 41, 50, or 52 moles of ATP, respectively. Moreover, even within halophytes themselves, species differ in succulence and in the solutes they accumulate, Chenopodiaceae being more able to use salt ions in osmotic adjustment than Poaceae (Flowers

and Colmer 2008). Succulence results in an increase in cell size and a decrease in growth extension, this process reduces surface area per tissue volume, leading to higher water content per unit area (Weber 2008).

Maintaining water status within plant tissues requires, in addition to osmotic adjustment, a decrease in water losses through a decline in stomatal conductance (*gs*). Nevertheless, differences between halophytes were described. For instance, in a comparative study between two obligate halophytes *Sesuvium portulacastrum* (C_3) and *Tecticornia indica* (C_4), different stomata responses were observed at moderate salt concentration (200 mM NaCl); in the former *gs* was enhanced whereas in the latter it showed no variation. At higher salt concentration (400 mM NaCl), this parameter was decreased in both species. The decrease in *gs* constitutes an identical early response to water and salt stress (Munns 2002). Indeed, plant responses to salt stress occur in two phases: a fast osmotic phase (whose period depends on species and stress severity) due to the increase in external osmotic pressure followed by a slower ionic phase due to ion accumulation in leaves (Munns and Tester 2008). Water use efficiency ($WUE = A / E$ with A and E standing respectively for net CO_2 assimilation and transpiration rate) was shown to be a good tool for measuring the aptitude of a plant to adjust its gas exchanges under stressful conditions by increasing CO_2 capture and reducing water losses (Gleick et al. 2011).

Vacuole sequestration is not limited to salt ions but it is also extended to a variety of toxic ions and molecules such as heavy metals (Hossain et al. 2012) and organic pollutants (Tissut et al. 2006). In the case of heavy metals, a prior chelation phase is needed (Mendoza-Cózatl et al. 2010). As regards organic pollutants, three phases are often described: 1) biotransformation that converts xenobiotics into more polar compounds (in some cases, this phase is not necessary), 2) conjugation that adds to the xenobiotics sugars, amino acids, or peptides to facilitate their metabolism, and 3) sequestration of conjugated molecules into vacuoles or their fixation to the cell wall components (Tissut et al. 2006).

2.1.2. Excretion of toxic molecules

Many halophytes were shown to have trichomes or salt glands controlling salt accumulation in plant tissues. Salt glands are embedded in the leaf epidermis. They can be multicellular, as observed in Dicots (Plumbaginaceae and Tamaricaceae), or bicellular, as reported in Monocots (Poaceae; Barhoumi et al. 2008). Trichomes are composed of two parts: *i)* a stalk embedded in the epidermis bearing *ii)* a unicellular bladder cell with a huge vacuole, a well-reduced cytoplasm pushed close to the wall, and only a few organelles (Smaoui et al. 2010). In some cases, salt excretion is performed by leaf cuticle as described in *Suaeda fruticosa* (Chenopodiaceae), a species with no excreting glands or trichomes (Labidi et al. 2010). Hence, salt excretion is a phenomenon by which halophytes eliminate excess salt reaching their leaves (Sobrado 2002) in a highly-selective way, secreting

mostly NaCl and thus contributing to maintain a suitable K^+/Na^+ ratio of cell cytoplasm. However, other ions such as K^+, Mg^{2+}, Ca^{2+}, and SO_4^{2-} can be excreted (Sobrado and Greaves 2000) if they are in excess in leaf tissues. Manousaki and Kalogerakis (2011) reported also that salt glands and trichomes on leaf surfaces of some halophytes (such as *Tamarix smyrnensis, Atriplex halimus, Armeria maritime, Avicennia marina, Avicennia germinans,* and *Spartina alterniflora*) can excrete excess metals as a possible detoxification mechanism.

2.1.3. Nutrient homeostasis

Nutrient homeostasis is one of the major factors allowing halophytes to survive under extreme saline conditions. It is based on two main strategies: nutrient uptake efficiency and nutrient use efficiency. Since the most abundant salt is NaCl, the former strategy relies on cation/Na^+ selectivity and anion/Cl^- one that increase to mitigate the salt-induced reduction in nutrient uptake efficiency (Hafsi et al. 2007; Rabhi et al. 2010c). However, K^+/Na^+ selectivity is the most studied one as this macronutrient is often more affected by salinity than other nutrients. Although nutrient/salt selectivity is often described in halophytes in response to salt stress, it is not sufficient to maintain nutrient uptake efficiency at the level of the control. This is why high use efficiency is needed (Hafsi et al. 2007; Rabhi et al. 2010c). Mineral nutrition is imbalanced by several stresses other than salinity. For instance, the two halophytic *Aeluropus* species *A. lagopoides* and *A. littoralis* displayed an increase in K^+ and Na^+ concentrations under drought stress (Vaziri et al. 2011). This is important for osmotic adjustment during water stress as inorganic osmolytes increase osmotic potential. Gulzar et al. (2003) who observed an enhancement in K^+ level in *A. lagopoides* tissues attributed such a response to drought stress to a high selectivity for K^+ by retaining higher Cl^- and Mg^{2+} ions in roots. Heavy metal stress is also a factor of nutrition disturbances and plants able to maintain their nutrient homeostasis under this stress are thought to overcome it. For instance, the two halophytes *Sesuvium portulacastrum* and *Mesembryanthemum crystallinum* experienced different potassium and calcium status as subjected to a range of cadmium (Cd) concentrations (0, 50, 100, 200, and 300 µM), the former being more able to maintain its nutrient homeostasis than the latter (Ghnaya et al. 2007). This was due to the fact that *S. portulacastrum* displayed a higher aptitude to produce biomass and to limit Cd uptake even under severe stress conditions than *M. crystallynum* (Ghnaya et al. 2007), which is probably due to its higher Ca^{2+} and K^+ selectivity over Cd^{2+}. In addition, recently, Zhan et al. (2013) found that a K^+ influx/H^+ efflux reaction is coupled with the transport of the Polycyclic Aromatic Hydrocarbon (PAH) phenanthrene into root cells, which constitutes a new insight into its uptake by plant roots. This also opens new perspectives on the role of nutrient homeostasis in plant tolerance to organic pollutants, in particular in halophytes.

2.1.4. Membrane integrity

Plant cells contain many membrane systems that are not considered as simple barriers delimiting different compartments; they are specialized to particular functions undertaken by their lipid components and membrane-associated proteins (Komatsu et al. 2007). Hence, almost all plant responses to environmental stresses directly or indirectly require membrane integrity to be maintained, although stresses themselves cause significant intracellular restructuring (Buchanan et al. 2000). The most studied membranes under abiotic stress conditions are plasmalemma, tonoplast, and thylakoid membranes. Plasmalemma plays structural and communicating (interface with the extracellular environment exchanging information and substances) roles. Hence, it constitutes the site of signal processing in response to stresses (Komatsu et al. 2007). To estimate membrane integrity under stress, some usual parameters are often used: *i)* malondialdehyde (MDA) concentration that constitutes an indirect measurement of lipid peroxidation (for all membranes), *ii)* electrolyte leakage that indicates the degree of the plasmalemma permeability and therefore its inaptitude to retain electrolytes (for plasmalemma since it is the last membrane to be crossed, *iii)* the correlation between excessive salts within a tissue and its water content to estimate the degree of their sequestration into vacuoles (for tonoplast), and *iv)* chloroplast ultrastructure that illustrates the degree of damage in grana (for thylakoid membranes). In halophytes, as in all plants, the use of these parameters among others have shown that a variety of severe abiotic stresses induce membrane damages (Ben Hassine et al. 2009; Parida and Jha 2013), which is due to the generation of Reactive Oxygen Species (ROS) responsible for oxidative stress (Bose et al. 2013). Hence, ROS homeostasis is one of the major factors allowing halophytes higher salt tolerance in comparison with glycophytes (Bose et al. 2013).

ROS overproduction was described in halophyte responses to several abiotic stresses as reviewed by Jithesh et al. (2006). It is initiated by the univalent reduction of O_2 or the transfer of excess excitation energy to O_2. The transfer of one, two, or three electrons generates respectively superoxide radicals ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), or hydroxyl radical ($HO^{\cdot}$) (Mittler 2002). Nevertheless, plants are equipped with two antioxidant systems that can scavenge ROS and therefore protect cell membranes and molecules from damages. The non-enzymatic system groups a variety of molecules such as tocopherol, carotenoids, ascorbate, and glutathione, whereas the enzymatic one groups several enzymes, namely superoxide dismutase, catalase, ascorbate peroxidase, monohydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase (Jithesh et al. 2006).

Chloroplast (thylakoid membrane) is one of the main targets of ROS. Its protection is therefore a priority in halophytes under stress conditions. Rabhi et al. (2010b) showed that the halophyte *Sesuvium*

portulacastrum is able to protect thylakoid membranes and proteins even at 400 mM NaCl. Similar results were also found in the halophyte *Sulla carnosa* under magnesium deficiency conditions (Farhat et al. 2014, 2015) as well as under individual and combined effects of salinity and iron deficiency (Unpublished data).

2.2. Biochemical and molecular mechanisms of cross-tolerance

2.2.1. Gene duplication and promoter adaptation

Gene duplication is a kind of genome adaptive mechanisms to environment fluctuations (Kondrashov 2012). The identification of copy-number variations (CNVs) in response to stressful or changing conditions may help understand gene duplications as an adaptive mechanism. Studies of 80 *Arabidopsis thaliana* ecotypes showed that natural selection has led to CNVs covering 2.2 Mb of the reference genome (Cao et al. 2011). The genomes of *A. thaliana* and its halophyte relative *Thellungiella parvula* have approximately 10% of their total genes in tandem duplicates (Dassanayake et al. 2011), and they are clearly involved in the species dramatically different stress tolerance strategies. This is exemplified by the amplification of *NHX8* homologs, known to encode a putative Li^+ transporter in *A. thaliana* (An et al. 2007). The duplication led to a constitutively higher expression in *T. parvula* than in *A. thaliana*. This was probably responsible for the improvement of *T. parvula* tolerance to high Li^+ concentrations in its natural biotope. Some other examples were also reported such as the duplications of *CBL10* orthologs, encoding a calcium sensor, *AVP1*, encoding a vacuolar proton transporter in *T. parvula*, and *HKT*, present in a single copy in *A. thalina* and in three ones in *T. parvula* (Dassanayake et al. 2011).

Based on molecular and genomic studies, several key transcription factors were identified to be induced under several abiotic stress conditions. Among them, DREB and ABF are well characterized transcription factors known to play an important role in regulating gene expression in response to abiotic stresses through both ABA-independent and dependent pathways. In parallel, many salt-induced promoters are not specific to salinity. Promoters of the stress-induced genes contain cis-regulatory elements such as DRE/CRT, ABRE, MYC recognition sequence (MYCRS), and MYB recognition sequence (MYBRS), which are regulated by various upstream transcriptional factors (Mahajan et al. 2005; Zhu 2002). Nawaz et al. (2014) compared expression levels and promoter activities of candidate salt tolerance genes in the halophyte *T. salsuginea* and the glycophyte *A. thaliana* using promoter swap experiments. They showed that SOS1 and VATD promoters were respectively five-fold and two-fold more active in *T. salsuginea* than in *A. thaliana*. These observations were supported by an expression of a higher number of gene families nonspecific to salt stress in the halophyte than in the glycophyte (Wu et al. 2012).

2.2.2. Wide genome transcriptional adaptation to abiotic stresses

Wu et al. 2012 found that 21 transcription factor families were expanded in *T. salsuginea* genome as compared to that of *A. thaliana*. These expansions may be associated with the adaptation of *T. salsuginea* to extreme environments, as individual members of some *A. thaliana* factor families have been shown to be related to stress tolerance. For example, the RAV gene family that has been reported to respond to several stresses, including salinity (Fowler et al. 2005; Sohn et al. 2006), expanded from six members to nine, respectively in *A. thaliana* and *T. salsuginea* (Wu et al. 2012). In the extreme halophyte *Salicornia brachiata*, transcript profiling revealed an abundance of *Sb*USP (an uncharacterized universal stress protein gene) transcripts in response to salt stress as well as to drought, heat, and cold stresses. Heterologous expression of this gene conferred salt and osmotic tolerance to *E. coli* (Udawat et al. 2013). Some other salt-responsive genes cloned from this halophyte experienced also elevated expression under abiotic stress conditions in the host plant. For instance, *Sb*MT-2 gene was up-regulated by salinity, drought, and heat stresses and its expression increased with treatment time (Chaturvedi et al. 2012). The peroxisomal ascorbate peroxidase gene (*Sb*pAPX) was also strongly induced by cold (Singh et al. 2013). In addition, pAPX gene cloned from *Avicenia marina* was up-regulated by salinity, H_2O_2, prolonged light, and ferric citrate treatment (Kavitha et al. 2008). In the same context, a SUMO conjugating (Small Ubiquitin related Modifier) enzyme gene 'SaSce9' from experienced induced transcripts under salinity, drought, cold, and exogenously supplied ABA conditions in leaves as well as in roots of the halophytic grass *Spartina alterniflora*. Its constitutive overexpression in *A. thaliana* improved its tolerance to salinity and drought (Karan and Subudhi 2012). In the halophyte *Limoniastrum monopetalum*, El-Bakatoushi (2011) showed that crude oil exposure over-expressed salt and drought genes.

2.2.3. *Proteomic analysis revealed the induction of several non specific-stress- and defense-related proteins*

While addressing the key pathways regulating abiotic stress plant adaptation, comprehensive data presented confirmed that proteins are relevant tools to confer tolerance. Therefore, it has been found out that salinity induces more proteomic changes in *A. thaliana* than in *T. salsuginea* (Oliver et al. 2011; Gechev et al. 2012; Dooki et al. 2006). The former displayed 88 differentially abundant protein spots *versus* 37 ones in *T. salsuginea* as compared to their controls (Dooki et al. 2006). Therefore, salinity changes more the proteomic profile of *A. thaliana* as compared to that of *T. salsuginea* since the latter is able to maintain enough photosynthetic activity and ATP production for stress adjustment. A proteomic study of *Suaeda salsa* under individual and combined

effects of salinity and heat shock showed that out of 80 proteins whose levels were increased by salt stress and 70 proteins whose levels were reduced by heat shock, an overlap of only 17 proteins was detected. In addition, out of 112 proteins accumulated by the combined effects, only 43 were salt-elevated and 30 were heat shock-elevated (Li et al. 2011). Hence, among 124 induced proteins (during salinity, heat shock, or their combination), only 14 were common in the three treatments (Li et al. 2011). Interestingly, the authors found an overexpression of STO5 not only by salt stress but also by heat shock and their combination, which can lead to higher salt tolerance in transgenic plants (Nagaoka and Takano 2003). An aluminum-induced protein-like protein (AIPLP) that has been shown to be involved not only in aluminum stress response but also in other metal, wounding (Snowden et al. 1995), and drought stress responses (Oztürk et al. 2002), was induced in *Puccinellia tenuiflora* under 95 mM Na_2CO_3 treatment, which suggests that it might also contribute to its tolerance to Na_2CO_3 stress (Yu et al. 2013). In addition, a developmentally-regulated plasma membrane polypeptide (DREPPPM)-like protein that has been shown to be involved in cold acclimation and salt stress, increased under Na_2CO_3 stress. This protein may be associated with the Ca^{2+} signal transduction pathway in the seedlings of *Puccinellia tenuiflora* under Na_2CO_3 stress (Yu et al. 2013).

2.2.4. Cross-tolerance-enhanced abundance of protective proteins involved in photosynthesis activation and protein biosynthesis

Abiotic stresses negatively affect photosynthesis at different levels, altering both photochemichal and non-photochemical processes (Saibo et al. 2009). Nevertheless, plants have developed many adaptive strategies allowing them to cope with severe conditions (Zhu 2002; Saibo et al. 2009). Identification of photosynthesis-related proteins that are differentially abundant under drought and severe salt stress is very important. So far, many photosynthesis-related proteins exhibited an increase or decrease in response to these two stresses (Oliver et al. 2011; Vanhove et al. 2012; Aranjuelo et al. 2011). The comparison between halophyte and glycophyte proteins under salt stress reviewed by Kosová et al. (2013) reported an increase in PsbP, ferredoxin-NADPH reductase, OEE2, RubisCO activase, TPI, GAPDH, and Glucose-6-P dehydrogenase in glycophytes and an increase in LHC, OEE2, RubisCO LSU and SSU, RubisCO activase, D2, CP24, CP47, PSI subunit IV, carbonic anhydrase; SBP, and PGK. In response to salinity, non-salt-specific proteins can be accumulated. For instance, Chen et al. (2012) found an enhanced abundance in eleven heat-shock proteins (HSPs) in the halophyte *Nitraria sphaerocarpa* under saline conditions. Based on literature and their own results, the authors suggested an HSP/chaperone network in plants that responds to salinity. As subjected to salt stress, the halophytic plant

Puccinellia tenuiflora exhibited an increased abundance of tocopherol cyclase, a crucial enzyme in the biosynthesis of α-tocopherol in plants (Yu et al. 2011) conferring it higher stress tolerance. It is also known that free metal ions can catalyze ROS formation. Therefore, responses leading to the elimination of free metal ions were observed in salt-stressed plants (Kosová et al. 2013). Stress also results in an accumulation of several protective proteins as chaperones from HSP90 family, HSP70 family, and Hsc70 (heat-shock cognate) (Kosová et al. 2013). Other stress-protective proteins, such as osmotin and osmotin-like proteins, are involved in enhancing osmotic stress responses. PR-10 proteins respond not only to biotic, but also to abiotic stresses, such as drought, salt, cold, and oxidative stresses, and UV-irradiation (Agarwal et al. 2013).

2.2.5. Abiotic-stress-commonly-induced alterations in carbohydrate nutritional status

Sugar metabolism is a very dynamic process and its metabolic fluxes and concentrations highly fluctuate with development stage and in response to environmental stresses (Rolland et al. 2006). Under abiotic stress, glucose has an important role as osmolytes in maintaining cell turgor, stabilizing cell membranes, and decreasing protein degradation (Sharp et al. 2004). Non-reducing disaccharides such as trehalose can accumulate with higher levels in tolerant plants. Other sugars with no energetic role, such as the oligosaccharides raffinose and stachyose were accumulated in response to abiotic stress conditions such as drought, salinity, and extreme temperatures (Kaplan et al. 2004). Relevant physiological studies have shown that soluble carbohydrates, like glucose, fructose, sucrose, or fructans, significantly contribute to the mechanisms of adaptation to salt stress (Parida et al. 2002). Gil et al. (2011) studied sugar accumulation in five halophytes (*Juncus acutus, Juncus maritimus, Plantago crassifolia, Inula crithmoides,* and *Sarcocornia fruticosa*) and found that sucrose, and at a lower level, glucose and fructose were the most abundant sugars in *J. acutus* and *J. maritimus,* and sorbitol the only soluble sugar accumulated in *P. crassifolia*. In addition to their involvement in osmotic adjustment, soluble carbohydrates stabilize also proteins and membrane structure and protect plant cell against ROS, especially in halophyte species (Szabados and Savouré 2010; Boriboonkaset et al. 2013). Polyols and sugar alcohols like mannitol or sorbitol were also accumulated and linked to abiotic stress tolerance (Arbona et al. 2008). In addition to all cited roles, sucrose, fructose, and glucose play also pivotal roles as signaling molecules to abiotic stresses (Koch, 2004; Rolland et al. 2006; Ruan 2014).

2.2.6. Enhanced biosynthesis of organic osmolytes, phenolic compounds, and lignin

Under abiotic stresses, plants synthesize osmolytes like soluble sugars and amino acids that contribute to turgor maintaining by osmotic adjustment (Arbona et al. 2003; Arbona et al. 2008). In this context, it is interesting to

follow the synthesis and levels of osmolytes involved in stress tolerance such as amino acids, secondary metabolites, and regulatory metabolites (Arbona et al. 2013). Indeed, increases in Proline (Pro) content have been reported in response to a variety of abiotic stress conditions like salt stress (Yoshiba et al. 1995; Arbona et al. 2008), soil flooding (De Campos et al. 2011), drought (Arbona et al. 2008), and extreme temperatures (Kaplan et al. 2004). The target enzyme is a pyrroline-5-caboxylate synthetase (P5CS) (Arbona et al. 2008). Pro plays also a role in ROS scavenging (Arbona et al. 2003) as well as in DNA, membrane, and protein stabilization (Arbona et al. 2008). Polyamines (PA) also have protective ROS scavenging roles (Alet et al. 2012). A variety of abiotic stresses were shown to induce PA accumulation that was found to positively correlate with stress tolerance (Martin-Tanguy 1997; Bitrián et al. 2012). Putrescine (Put), spermidine (Spd), and spermine (Spm) are the most abundant PAs found in higher plants (Arbona et al. 2013). It has been recently reported that, in non-adapted *Thellungiella salsuginea* accessions, sugars and polyamines could be involved in the mechanisms of cold adaptation (Colinet et al. 2012). However, the most described and important compounds are sugars, sugar alcohols, and nitrogenous compounds with low molecular weight (in particular Pro and glycinebetaine). Their accumulation in adapted plants is thought to be involved in their tolerance to stresses (Witt et al. 2012). Under heavy metal stress, to reduce metal accumulation in photosynthetic organs is considered as a tolerance trait like phytochelatin biosynthesis and glutathione metabolism (Arbona et al. 2013).

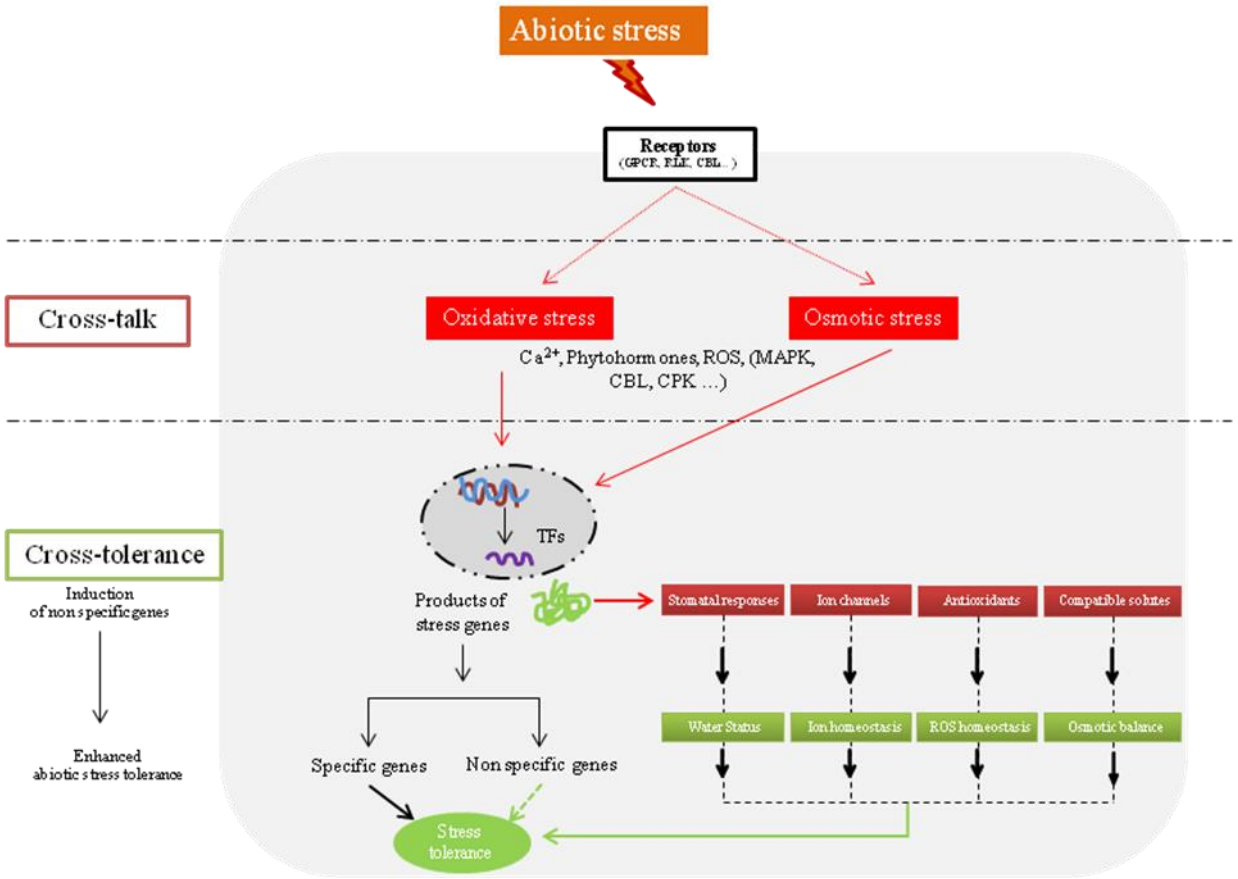
It is known that heat induces PAL activity and phenolic production and reduces, at the same time, their oxidation, contributing to heat stress acclimation (Arbona et al. 2013). The precursors of lignins, phenylpropanoids are also involved in stress defense mechanisms, in particular in roots where they can adjust cell wall composition and stiffness (Van Poecke et al. 2001; D'Auria et al. 2005).

Carotenoids and xanthophylls are lipophilic compounds synthesized in plants from isopentenyl pyrophosphate (IPP) *via* the plastidial methyl erythritol phosphate (MEP) pathway. The role of carotenoids is not restricted to cell protection from UV radiation under stress conditions. Indeed, it was demonstrated that the overexpression of phytoene synthase gene in transgenic tobacco plants resulted in a higher osmotic and salt tolerance, but through channeling carotenoid flux to ABA biosynthesis which resulted in an enhancement of ABA levels (Cidade et al. 2012).

The following diagram (Figure) summarizes specific and non-specific responses to combined stresses.

Figure. Schematic diagram showing the possible cross-talk involved in the response of halophytes to multiple stresses. The signal pathways resulting from several stresses induce specific and non-specific genes that can

confer stress-tolerance. The latter are responsible for cross-tolerance. GPCR: G-protein-coupled receptor; RLK: receptor-like kinase; CBL: calcineurin B-like interacting protein kinase; CPK: calcium-dependent protein kinase; MAPK: mitogen-activated protein kinase; ROS: reactive oxygen species; TFs: transcription factors.



3. Cross-tolerance between salinity and organic pollutants: application for phytoremediation

3.1. Compartmentalization and subcellular sequestration are common mechanisms involved in salinity and organic pollutant tolerance

As heavy metals and salts, organic pollutants constitute one of the major hazardous chemicals that contaminate soils today (El-Bakatoushi 2011). The uptake of toxic organics in plant cells and/or their sequestration or metabolism are essential for detoxification of the rhizosphere and in turn for phytoremediation. Therefore, organic pollutants such phenanthrene may passively penetrate the plasmalemma of root and shoot cells (Alkio et al. 2005). Wild et al. (2004) traced the movement of anthracene in maize leaves and showed that it was localized on the leaf surface; it diffused into the cytoplasm within 72 h. This finding was supported by Alkio et al. (2005) who showed that phenanthrene can diffuse in *Arabidopsis* through direct contact with the tissue as well as from the air. Also, Zhan et al. (2010) found in wheat two modes of phenanthrene transport; a simple diffusion and an active absorption by a transporter. In the same context, Cobbett and Meagher (2002) reported that the uptake of organic xenobiotics into the plant cell is often mediated by an ABC transport protein. A subclass of the ABC transporters**,** originally named the multi drug resistance proteins (MRPs) in reference to animal cells and bacteria, is the best-characterized family of plant proteins that carry organics across membranes. MRPs are involved in the uptake, efflux, and sequestration of toxic compounds and xenobiotics (Tommasini et al. 1998). In literature, little is known about the mechanisms of Polycyclic Aromatic Hydrocarbon (PAH) metabolism and accumulation in plants. All authors used the green lever model to explain plant cell internalization, degradation, and sequestration of organic compounds such as PAHs (Sandermann 1992). In plants, the metabolism of xenobiotics can be divided into three phases leading to the neutralization of the organic pollutant: transformation (Phase I), conjugation (Phase II), and compartmentalization (Phase III) (Sandermann 1992). The first two phases are similar to those used by animals. During phase I, the compound is transformed by oxidation (frequently), reduction, or hydrolysis, creating one or more functional groups on the molecule (Komives and Güllner 2005). The hydrophobic character of organic pollutants like PAHs suggests hydroxylation by specific enzymes to transform them into hydro-soluble compounds in cytoplasm. Hence, in phase II, one or more substituents are attached onto endogenous or existing active sites formed during Phase I. The main reactions include conjugation of glycosides, glutathione, amino acid, or malonic acid. During phase III, the soluble compounds are either stored in the vacuole or incorporated into lignin or other cell wall components of becoming non-extractable. Due to its similarity with the hepatic detoxification mechanisms in animals, the term "green liver" has been adopted for the operation of plant cells during xenobiotic metabolism (Sandermann 1994). This concept was supported

by Alkio et al. (2005) who demonstrated that in *A. thaliana*, phenanthrene was detected and sequestrated in particular cell "trichomes" and after higher amount of PAHs it was diffused to basal unclear cells, with increased the levels of particular mono- or dioxygenases that allow increased tolerance and transform PAHs to non-toxic intermediate compounds during phase I (Cerniglia 1997; Kanaly and Harayama 2000).

Similarly, since monovalent ions, used by halophytes and salt-tolerant glycophytes for osmotic adjustment, are toxic at the required concentrations, Na^+ and Cl^- are predominantly vaculole-compartmentalized to maintain their concentrations in the cytoplasm within tolerable limits (Whyn Jones and Gorham 2002). Although the evidence is limited, Na^+/H^+ exchange and the activity of one or more of the PMF-generating enzymes appear to play a role in the accumulation of Na^+ as they increase under saline conditions. However, ion transport across tonoplast is not sufficient for efficient compartmentalization; their retention within vacuoles is also required and was shown to be correlated with low tonoplast fluidity (Leach et al. 1990). Hence, one can speculate that since halophytes are more efficient in saline ion compartmentalization than glycophytes, they are theoretically more able to sequester any other toxic ion or compound.

3.2. ROS accumulation and signaling are common features shared between stresses induced by salinity and organic pollutants

Liu et al. (2009) suggested that phenanthrene oxidized by mono- or di-oxygenases, like the CYP, increased ROS level, which induces oxidative stress. However, it cannot be confirmed if oxidative stress is a consequence of phenanthrene detoxification activities or of its own or derivative phytotoxicity (Liu et al. 2009). ROS production is an unavoidable event for all organisms exposed to oxygen and Na^+ and Cl^- accumulation in the cytosol increased ROS production (Allakhverdiev et al. 2002). The result of hydroxylation of organic pollutant by cytochrome P450 generated also ROS production. A higher antioxidant capacity in halophytes than in glycophytes has been suggested to confer them a higher tolerance to stresses such as salinity (Flowers and Colmer 2008; Kosová et al. 2013) and phenanthrene toxicity (Shiri et al. 2014). Mittler (2006) reported that the exposure of a plant to a combination of several abiotic stresses will co-activate different stress-response pathways. The results of stress combination have a synergistic or antagonistic effect. This suggests that a cross-talk between co-activated pathways is likely to be mediated at different levels. These could involve a variety of transcription factor networks, mitogen-activated protein kinases (MAPK) (Cardinale et al. 2002; Xiong and Yang 2003), a multitude of stress hormones (ethylene, jasmonic acid, and abscisic acid) (Anderson et al. 2004),

calcium and/or ROS signaling (Mittler et al. 2004; Bowler and Fluhr, 2000) as well as numerous receptors and signaling complexes (Casal 2002).

The stress tolerance by increasing antioxidant activity is attractive to explain a high tolerance in halophytes to organic pollutants that generated an oxidative stress (Liu et al. 2009). Therefore, the higher levels of enzymatic antioxidants in halophytes, in particular that of SOD, suggest that the crucial role to rapid conversion of $O_2^{\cdot -}$ to H_2O_2 may be essential for early defense signaling. Halophyte species induced rapidly H_2O_2 levels, then they have higher SOD level 'in stock' (Bose et al. 2011). Secondly, high levels of APX and CAT may interfere with H_2O_2 signaling and decrease its positive role. However, only $OH^{\cdot}$ is highly reactive and causes significant damage to cell structures and is the major compound resulting from hydroxylation of PAHs, it is also known to activate directly a range of Na^+, K^+, and Ca^{2+}-permeable cation channels (Demidchik et al. 2010; Zepeda-Jazo et al. 2011) disturbing K^+/Na^+ ratio within cytoplasm and inducing programmed cell death (PCD) (Shabala et al. 2007; Shabala, 2009; Demidchik et al. 2010).

3.3. The understanding of salinity and organic pollutant tolerance may help improve phytoremediation

Phytoremediation is known as a green technology using plants to remediate contaminated-environments. It is cheap, non-instructive, and effective means of pollutant cleanup. In literature, little is known about halophyte use in phytoremediation of organic pollutants. The majority of the examples of phytoremediation by halophytes was reported in salt marshes, their natural habitats (Howes Keiffer and Ungar 2002; Al-Mailem et al. 2010; Masciandaro et al. 2014; Ribeiro et al. 2014). Salt marshes constitute important ecosystems severely exposed to risks due to the oil spills resulting from accidental discharges, leakage from boats, industrial wastewater discharges, and urban runoff (Ribeiro et al. 2014). Phytoremediation of organic pollutants is based on the observation that planted contaminated soil *versus* unplanted soil showed on acceleration of organic pollutant degradation in the presence of plants (Burken and Schonoor 1996; Masciandaro et al. 2014). There are two different strategies of phytoremediation: *direct* and *explanta* phytoremediation (Salt et al. 1998). The first one consists of pollutant uptake by analogy to phytoextraction of heavy metals. However, the availability of organic pollutants depends on their physicochemical properties and their concentration in soil (Wenzel et al. 1999). The second one is based on exudates synthesized by roots like enzymes involved in the degradation of organic pollutants and other compounds stimulating fungi and bacteria growth that use pollutants as carbon source.

In this context, phytoremediation of organic pollutants remains unexplored enough. The majority of investigations in this field focused on the interaction between microorganisms and roots to improve the

degradation of organic pollutants in soil. Some studies reported that PAHs can be taken up by plant leaves from air or by their roots from soil (Simonich and Hites 1994; Kipopoulou et al. 1999; Fismes et al. 2002). Indeed, because of their high lipophily, they are adsorbed either on leaf cuticle and passed through it by solubilization in waxes or on root suberine cortical zones and absorbed by root cells (Simonich and Hites 1994; Kipopoulou et al. 1999; Fismes et al. 2002). The halophyte *Halocnemum strobilaceum* naturally inhabiting hypersaline soils was shown to remediate soil contaminated by aromatic hydrocarbon in the Arabian Gulf (Al-Mailem et al. 2010). A 'phytoremediation' culture of *Cakile maritima* on sterilized sand (without microorganisms) contaminated with phenanthrene significantly decreased its phytotoxicity in a subsequent culture of *Thellungiella salsuginea* (Shiri et al. 2015). Meudec et al. (2005) investigated also the uptake of fuel oil PAHs by the halophytic plant *Salicornia fragilis* and the bioaccumulation of these compounds into shoot tissues in the upper aerial part of the plant. This finding proves that plants are able to take up and to accumulate PAHs in their biomass. This bioaccumulation depends on the time and dose of exposure to fuel oil in the sediment. In this example of halophytic plant, the uptake by roots of PAHs seems to be the main pathway. The particular morphology of *Salicornia* plants (no real leaf) and the absence of PAHs in control also suggest that PAHs detected are not originated from atmospheric contamination. The different PAH distribution suggests that low molecular weight PAHs, like phenanthrene and pyrene due to their higher solubility, are transported more easily in the phloem than high molecular weight PAHs like benzo(a)pyrene. Fismes et al. (2002) reported that the transport of low molecular weight PAHs from root to aerial parts could be passive and driven by transpiration flux.

4. Concluding remarks

Halophytes are of significant interest since they naturally occur in environments with excess toxic ions and research findings suggest that they also tolerate other abiotic stresses through cross-tolerance mechanisms that allow them tolerance to several stresses in addition to salt stress tolerance. In this review, we focused on cross-tolerance mechanisms in halophytes at the physiological, genomic, transcriptomic, proteomic, and metabolomic levels with an emphasis on their cross-tolerance to salinity and organic pollutants. Their powerful subcellular sequestration of toxic ions and compounds and their high activities of antioxidant enzymes constitute key traits in their high tolerance to both salinity and organic pollutant stresses. However, data about halophyte use in the phytoremediation of organic pollutant-contaminated soils are scarce. Comparative studies between halophyte and glycophyte responses to these pollutants are encouraged. In addition, the effects of optimal salinity levels on halophyte phytoremediation potential of organic pollutants are particularly required.

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